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The Evolutionary and Ecological Significance of the Clutch Size of the Osprey (Pandion haliaetus)

Christopher Hall Stinson
College of William & Mary - Arts & Sciences

THE EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF THE CLUTCH SIZE OF THE OSPREY (*PANDION HALIAETUS*)

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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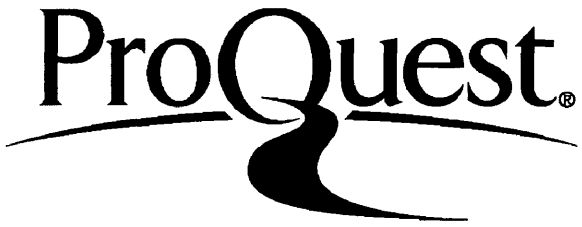
by

Christopher H. Stinson

1976



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Dear Dr. Stewart,

I am writing with regard to my M.A. thesis (1976), The Evolutionary and Ecological Significance of the Clutch Size of the Osprey (Pandion haliaetus), which was recently bound.

There are several typographical errors in the thesis; I would greatly appreciate it if you would insert a sheet in the thesis copies bring attention to the errors.

p. iv, line 17: "competance" should read "competence".

p. v, lines 1 and 5: "competance" should read "competence".

p. 42, line 22: "then" should read "They".

p. 44, line 11: "resource" should read "behavioral".

Also, it appears that p. 85 of the original manuscript was not included in the thesis copies. If you would insert a copy of p. 86 into the thesis copies, I would be most appreciative.

I regret that I did not discover these errors earlier, and thank you sincerely for your efforts to correct them. Please contact me if there is any difficulty.

Sincerely,

Chris Stinson

Christopher H. Stinson

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

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Author

Approved, August 1976

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for whatever competance I may have as an ecologist. Dr. Mitchell A. Byrd served as chairman of my graduate committee, supported and guided my research efforts, assisted with the field work, gave freely and unselfishly of his knowledge of ospreys, and is in large part responsible for whatever competance I may have as an ornithologist. I sincerely thank all of the above for their support, encouragement,.and assistance; this thesis would have been otherwise impossible.

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ABSTRACT

Ospreys (Pandion haliaetus) were observed for over 400 hours in 1975 in southeastern Virginia. Male ospreys, which procure essentially all of the food for the family unit once the chicks hatch, spend an average of 42.77% of the daylight hours perched near the nest when they have unfledged young. About 1/3 of the daylight hours are utilized for hunting. There is no correlation between weather conditions and the percentage of time the male was perched near the nest. Wind speed variability was positively correlated with the length of time between the departure of the male from the nest site and his return with a fish (mean time = 0.63 hr/fish), but accounted for only 16% of the variation in length of hunting trips. The rate at which the male brought fish to the nest (mean = 0.51 fish/hr) varied slightly with weather conditions (variation in weather conditions accounted for 16% of the variation in the rate at which fish were brought to the nest). The rate at which fish were brought to the nest was not correlated with either brood size or the age of the young. As the chicks age, the male spends more time away from the nest; this is not correlated with changes in weather, and appears to be due to decreasing attentiveness at the nest site on the part of the male.

When the young ospreys have fledged but are still dependent on their parents for food, the 2 adults together bring as much fish to the nest as the male alone brought to the unfledged young. Adults with fledged but dependent young spend an average of 1/3 of the day perched near the nest. Both the percentage of time that an adult with fledged young perches near the nest and the rate at which an adult with fledged young brings fish to the nest are negatively correlated with relative humidity. However, in both cases, relative humidity accounted for less than 10% of the variation in the dependent variable.

David Lack has argued that if evolution by means of natural selection has optimized reproductive output, then birds with nidicolous young should lay a clutch which corresponds to the largest number of healthy young which usually can be fed adequately by the parents. However, there seems to be no explanation which is consistent with both Lack's hypothesis and my observations, of the fact that male ospreys with unfledged young spend over 40% of the daylight hours perched near the nest. Additionally, none of the traditional alternatives to Lack's hypothesis (e.g., group selection) seem any more adequate for explaining the fact that male ospreys with unfledged young to feed spend over 40% of the day perched near the nest. Population ecologists have traditionally assumed that life history patterns evolve by hard selection (which selects only for optimal life history patterns), but it seems that ospreys have a life history pattern which has evolved by soft selection (which would select for operational life history patterns). Thus, the assumption of optimizing evolution in attempts to explain life history patterns of all organisms does not appear to be always valid.

THE EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF THE CLUTCH SIZE OF THE OSPREY (*PANDION HALIAETUS*)

INTRODUCTION

The question of which factors are ultimately (evolutionarily) responsible for determining the clutch size of bird species has received wide review and study. At least after Phillips' (1887) demonstration that some birds were capable of laying more eggs than were ever present in a complete clutch, it became generally accepted that birds laid only as many eggs as they needed young to counter the mortality experienced by the population (Lack 1954). David Lack (1954, 1966, and elsewhere) has argued against that concept by pointing out that if evolution by means of natural selection causes the survival of the fittest individuals (those who produce the largest number of healthy young [Fisher 1958]), birds should be laying a clutch which corresponds to the largest brood which usually can be successfully reared. Lack further argued that, for birds with nidicolous young, the usual clutch size should correspond to the largest brood which usually can be fed adequately by the parents.

In initial studies during the spring and summer of 1974, I spent slightly over 98 hours in southeastern Virginia observing ospreys (Pandion haliaetus) at their nests. About 62 of those hours were spent watching nests where there were unfledged chicks. At those nests, the male osprey (who procured essentially all of the food for the family unit once the chicks had hatched) spent about

60% of his time perched near the nest. Flights where the male flew from the nest and returned with nothing or with nesting material occupied 19% of the observed hours. Flights where the male flew from the nest and returned with a fish occupied only 21% of the observed hours. The number of chicks in the nest did not seem to have any effect on the amount of time the male spent away from the nest.

For Lack's hypothesis to be correct, all birds must be producing the maximum number of healthy offspring possible. If the male osprey can provide food for his offspring in 21-40% of the daylight hours, it seems plausible that he could rear a much larger family by utilizing a greater proportion of the day for hunting. If it is indeed possible for ospreys to rear a brood which is larger than their usual clutch size, then Lack's hypothesis is incorrect. The purpose of this study of the osprey in southeastern Virginia was to test the validity of Lack's hypothesis that birds with nidicolous young lay a clutch which corresponds to the largest brood they can adequately feed.

METHODS AND MATERIALS

A total of 20 active osprey nests which could be observed from accessible sites, and/or which could be visited to weigh and band the chicks after they hatched were located for study. Throughout this study, I distinguish between "observing" and "visiting" a nest. "Visiting" refers to going to the nest, usually to weigh the chicks. "Observing" refers to sitting at least 25 meters away from the nest at all times, usually to record the behaviors of the adults and the chicks. Although I never observed from a blind, I never felt that my presence was causing any substantial modification of the ospreys' behavior. A few times the birds seemed to be temporarily distressed by the unfamiliar presence of a human, but they quickly (within a few minutes) disregarded my presence. The osprey nests discussed in this study are described in greater detail in Appendix I.

I observed ospreys at 8 nests for over 98 hours between 14 April and 10 July 1974, and at 14 nests for over 408 hours between 9 March and 19 August 1975. When I observed a particular nest, I sat on the shore (all nests which were observed were over water) near the nest and observed the nest through a 30x telescope. The distance from the observer to the nest ranged from 25 meters to about 200 meters (mean = 50 m), except that nest 8, observed

briefly in 1974, was about 800 meters away. Flights from the nest by either of the adults or by the young were followed with 8x30 binoculars as long as the bird was in sight. I recorded in a notebook all events as they happened. During my 1975 observations, I recorded on the quarter-hour the percentage of sky which was covered by clouds ("cloudiness"), whether it was overcast or sunny ("sunniness"), the amount of precipitation which had fallen during the preceeding 15 minutes, the maximum wind speed and the minimum wind speed (miles/hour) which had occurred during the preceeding 15 minutes, and the wet-bulb and dry-bulb temperatures. Sunniness was recorded as 100% if the preceeding 15 minutes had been completely sunny (i.e., shadows were continuously visible), as 50% if the preceeding 15 minutes had been intermittently sunny, and as 0% if the preceeding 15 minutes had been overcast (i.e., no shadows were visible). Precipitation was measured in a plastic rain guage. Wind speeds were visually estimated on the basis of the wind-speed charts in Donn (1972, p. 439); "modal" wind speed was calculated as the average of the maximum and minimum wind speeds recorded each quarter-hour. Wet-bulb and dry-bulb temperatures were measured with a Bendix motorized psychrometer, and relative humidity was calculated from these as described in Appendix II. Additionally, I calculated the tide stages from appropriate tide tables (U.S. Department of Commerce 1975). Since the United States was on Daylight Savings Time on the dates when this study was being carried out (DeLury 1975, p. 785), one hour was added to the times (Standard Time) in the tide tables.

From 30 May through 14 August 1975, I visited 12 osprey nests (11 of which I was also observing) at intervals of about one week to weigh the chicks in the nests. The age of the chicks was estimated within several days of hatching, with the exception of nest 25 where 3 of the young were about 14, 16, and 18 days old on my first visit to the nest. At each visit, I weighed the chicks with Pesola spring scales and recorded the weights; once the chicks were banded (as described below), the band weights were subtracted from all subsequent weights.

With the assistance of Dr. Mitchell A. Byrd of the College of William and Mary, all chicks were banded at about 21 days of age with a U.S. Fish and Wildlife Service (FWS) numbered aluminum band and 3 colored plastic bands. The aluminum FWS band and the 3 colored bands were arranged in a combination (2 bands on each leg) which was unique for each chick. That permitted subsequent individual identification of each chick.

In 1975, the brood size at 2 nests was increased by introducing new chicks from nearby nests. Nest 25 on 31 May 1975 had 4 chicks which were approximately 7, 14, 16, and 18 days old; a fifth chick which was 8 days old was introduced. Nest 38 on 30 May 1975 had one egg and 2 chicks which were 1 and 3 days old; 2 chicks 3 and 4 days old from 2 nearby nests were transferred to nest 38. On 3 June 1975, nest 38 was revisited and the egg was found to be addled; a fifth chick 4 days old from a nearby nest was added to the brood.

Multivariate and univariate regressions and correlations,

analyses of variance, and Duncan's multiple range test were calculated on the College of William and Mary's IBM 370 computer using the appropriate programs in the Statistical Analysis System (Barr and Goodnight 1972). Bartlett's test for the heterogeneity of variances and an approximate test for the equality of means when the variances are unequal, were calculated after Sokal and Rohlf (1969).

In all multivariate correlations where the dependent variable was either the average rate (fish/hour) at which fish were brought to the nest in each 4-hour period of the day or fraction thereof (05:00-09:00, 09:00-13:00, 13:00-17:00, and 17:00-21:00 Daylight Savings Time), or the percentage of time which a particular adult was perched near the nest during each period of the day (or fraction thereof), the Stepwise Regression procedure (Barr and Goodnight 1972) was used to derive the best correlation with the following independent variables: the number of chicks in the nest, the average age (days) of the chicks in the nest, the maximum and minimum wind speeds (miles/hour) recorded each 4-hour period (or fraction thereof), the average difference between the maximum and minimum wind speeds recorded every quarter-hour, the average "modal" wind speed (miles/hour), the average dry-bulb temperature (^{o}C) recorded every quarter-hour, the average relative humidity (%) recorded every quarter-hour, the average cloudiness recorded every quarter-hour, the average sunniness recorded every quarter-hour, the average rate (mm/.25 hour) at which precipitation occurred,

the percentage of 15-minute segments which were completely (100%) sunny, and the percentage of 15-minute segments during which some precipitation occurred.

In the multivariate correlations where the dependent variable was the length of time (hours) the male was absent from the nest site when he left the area with nothing and returned with a fish, the Stepwise Regression procedure (Barr and Goodnight 1972) was used to derive the best correlation with the following independent variables: the number of eggs in the nest, the average age of the chicks in the nest, the number of young in the nest, the average maximum and minimum wind speeds recorded every quarter-hour during the male's absence, the average difference between the maximum and minimum wind speeds recorded every quarter-hour during the male's absence, the average "modal" wind speed during the male's absence, the average dry-bulb temperature during the male's absence, the average relative humidity during the male's absence, the average cloudiness recorded every quarter-hour during the male's absence, the average sunniness recorded every quarter-hour during the male's absence, and the average rate of precipitation during the male's absence.

Exactly which variables should be included in the "best" correlation is presently an unsolved statistical problem (Marriott 1974, p. 104). I used the Stepwise Regression procedures of Barr and Goodnight (1972) to arrive at a set of potentially "best" correlations. As suggested by Marriott (1974, pp. 104-105), the

best correlation was selected as the correlation with the smallest residual sum of squares where all included variables were significant at about the 0.05 level (determined by partial F-test; see Draper and Smith 1967, pp. 71-72), and where all regression coefficients (β) were at least double their standard error.

RESULTS

Observations on Ospreys before Eggs Were Laid

On 9 March 1975, I spent about 7.4 hours observing a male osprey at its nest site before the female osprey had returned from the wintering grounds. During that time, the male caught and ate one fish; the bird was perched at the nest site for about 53% of the observed hours.

On 25 and 30 March 1975, I spent a total of about 25.5 hours observing a pair of ospreys at their nest site before any eggs were laid. During that time, the male spent about 59.5% of the observed daylight hours perched near the nest. During the 25.5 hours, 9 fish were brought to the vicinity of the nest (8 were caught by the male and one was caught by the female). The average length of time between the departure of an osprey from its perch and its return with a fish was 0.42 hours. No statistical analysis was attempted on this small sample of hunting trips, but my subjective impression is that weather was not affecting the birds' hunting performance any differently than later in the season.

Observations of Ospreys with Unfledged Young

From 2 June through 13 August 1975, I spent about 252 hours observing ospreys with unfledged young in their nests. On 7 June 1975, I spent 4 additional hours observing a pair of ospreys whose single young was dead; those observations are not included in the following discussion.

During the 252 hours when I observed ospreys with unfledged chicks, the male ospreys spent an average of 42.66% of the observed daylight hours perched near or at the nest. Flights where the male flew from the nest area with nothing and returned with a fish occupied 29.85% of the observed daylight hours (N = 117). Flights where the male flew from the nest area with nothing and returned with nothing occupied 9.79% of the observed daylight hours (N = 83). Flights where the male flew from the nest area with nothing and returned with nesting material occupied 3.04% of the observed daylight hours (N = 56). Flights where the male flew from the nest area with a fish (or partially eaten fish) and later returned with the same fish occupied 5.80% of the observed daylight hours (N = 46). Flights where the male left the nest area before I began observing, and returned with a fish occupied 2.89% of the observed daylight hours (N = 11). Flights where the male flew from the nest area with nothing and did not return before dusk occupied 4.21% of the observed daylight hours (N = 12).

Time use by male ospreys with unfledged young is summarized in Table I.

During the 252 hours when I observed ospreys with unfledged young, the female ospreys spent an average of 95.12% of the observed daylight hours at the nest. Flights where the female flew from the nest with nothing and returned with nothing occupied 1.95% of the observed daylight hours (N = 82). Flights where the female flew from the nest with nothing and returned with nesting material occupied 1.76% of the observed daylight hours (N = 68). Flights where the female flew from the nest with nothing and returned with a fish occupied 0.69% of the observed daylight hours (N = 3); none of those flights occured before the young were at least 38 days old. Time use by female ospreys with unfledged young is summarized in Table I.

The male osprey was responsible for capturing 98% of the fish which were brought back to nests containing unfledged young; the female osprey brought back only 2% of the fish captured while the chicks were unfledged. On the average, the male used 0.64 hours to fly from the nest area and return with a fish (117 fish brought to the nest in about 75.22 hours); since many of the fish brought to the nest by the male were partially eaten, the actual average time required to capture a fish is lower than that. The male brought fish to the nest at an average rate of 0.516 fish/hour (130 fish brought to the nest by the male in 252 hours). I estimate that the male spent an average of 5.12 hours/day hunting for fish

Table I.

Time use by male and female ospreys with unfledged young based on 252 hours of observation between 2 June and 13 August 1975.

		Male		Female	
		No.	% Time	No.	% Time
Behavior		Observations	Used	Observations	Used
present at or near nest		----	42.66%	----	95.12%
Left	Returned				
with nothing	with fish	117	29.85%	3	0.69%
with nothing	with nothing	83	9.79%	82	1.95%
with nothing	with nesting material	56	3.04%	68	1.76%
with fish	with same fish	46	5.80%	3	0.02%
with fish	with nothing	1	0.08%	1	0.46%
with fish	with different fish	2	0.81%	0	0.00%
with fish	with nesting material	1	0.31%	0	0.00%
unobserved	with fish	11	2.89%	0	0.00%
unobserved	with nothing	3	0.56%	0	0.00%
with nothing	unobserved (dusk)	12	4.21%	0	0.00%
			100.00%		100.00%

(assuming 15.5 hours of daylight each day, that is 0.516 fish/hour x 0.64 hours/fish x 15.5 hours/day). The male apparently spends about 33% of the daylight hours hunting. That conclusion is consistent with the fact that the flights where the male returned to the nest with a new fish took up 33.55% of the observed daylight hours.

There were no significant differences between the percentages of time that the male was perched near the nest in the 4 different 4-hour periods of the daylight hours (analysis of variance, $P > .9958$; see Table II). The 4 variances were not significantly heterogeneous (Bartlett's test, $.50 > P > .10$). Apparently, the time of day did not affect the amount of time the male spent perched near the nest in any consistent manner.

The only environmental variable which was significantly correlated with the percentage of time that the male was perched near the nest each section of the day was the average age (days) of the chicks in the nest ($P < .0002$; $\beta = -1.0 \pm 0.205$). The negative correlation accounted for about 26% of the variation in the percentage of time the male was perched near the nest (coefficient of correlation = 0.264).

There were significant differences between the rates at which the male brought fish to the nest during each of the 4-hour periods of the daylight hours (analysis of variance, $P < .0044$; see Table III). The 4 variances were not significantly heterogeneous (Bartlett's

Table II.

Means, standard errors, and number of observations of percentage of time that the male osprey was perched near the nest during each period of the day (or fraction thereof).

Period	Number of Observations	Mean	Standard Error
05:00-09:00	14	43.999 %	5.594 %
09:00-13:00	17	43.069 %	7.031 %
13:00-17:00	19	43.360 %	6.123 %
17:00-21:00	19	41.864 %	6.322 %
Overall Mean		43.006 %	

Table III.

Means, standard errors, and number of observations of rate (fish/hour) at which the males brought fish to their unfledged young in each period of the day (or fraction thereof).

Period	Number of Observations	Mean	Standard Error
05:00-09:00	14	0.7444	0.0663
09:00-13:00	17	0.3956	0.0744
13:00-17:00	19	0.5439	0.0493
17:00-21:00	19	0.4661	0.0650
Overall Mean		0.5266	

test, .50 > P > .10). The rate at which the male brought fish to the nest in the first period of the daylight hours (05:00-09:00) was significantly greater than the rate at which the male brought fish to the nest during the other periods of the day (Duncan's multiple range test, $P < .05$; see Table IV). The rates at which the male brought fish to the nest during the other periods of the daylight hours were not significantly different from each other (Duncan's multiple range test, $P > .05$; see Table IV).

The rate at which the male brought fish to the nest (fish/hour) was significantly correlated with the average rate of precipitation ($P < .0336$; $\beta = -0.6 \pm 0.28$), the average dry-bulb temperature (^{o}C) ($P < .0159$; $\beta = -0.03 \pm 0.01$), the average "modal" wind speed (miles/hour) ($P < .0129$; $\beta = 0.05 \pm 0.02$), and the maximum wind speed (miles/hour) recorded during the 4-hour period ($P < .0218$; $\beta = -0.03 \pm 0.01$). The correlation accounted for 16% of the variation in the rate at which the male brought fish to the nest (coefficient of correlation = 0.160). Surprisingly, neither the age nor the number of young in the nest were significantly correlated with the rate at which the male brought fish to the nest.

The length of flights (hours) when the male with unfledged young left the nest area and returned with a fish was significantly correlated with the average difference between the maximum and minimum wind speeds (miles/hour) recorded every quarter-hour ($P < .0002$; $\beta = 0.08 \pm 0.02$), the average age (days) of the chicks

Table IV.

Duncan's 5 percent level Multiple Range Test on the mean rate (fish/hour) at which the males brought fish to their nests in each of the 4 periods of the daylight hours.

Period of the Day	Mean	
05:00-09:00	0.7444	
13:00-17:00	0.5439	T
17:00-21:00	0.4661	+
09:00-13:00	0.3956	⊥

Note: the vertical line on the right connects mean rates which were not significantly different at P = 0.05.

in the nest ($P < .0002$; $\beta = 0.03 \pm 0.01$), the number of eggs in the nest ($P < .0130$; $\beta = 0.55 \pm 0.22$), and the number of chicks in the nest ($P < .0230$; $\beta = 0.09 \pm 0.04$). The correlation accounted for about 32% of the variation in the length of hunting trips (coefficient of correlation = 0.317); the average difference between the maximum and minimum wind speeds recorded every quarter-hour accounted for 16.5% of the variation in the length of hunting trips.

There was no difference in the mean length of time between when the male left the nest area with nothing and when he returned with a fish during each of the 4-hour periods of the daylight hours (approximate test for the equality of means, $.25 > P > .10$); the 4 variances were significantly heterogeneous (Bartlett's test, $P < .005$; see Table V). There was no significant difference in the length of time required to catch a fish during each of the 4 quarters of the tidal fluctuations (low tide to mid-tide, mid-tide to high tide, high tide to mid-tide, and mid-tide to low tide) (analysis of variance, $P > .9958$); the 4 variances were not significantly heterogeneous (Bartlett's test, $.90 > P > .50$; see Table VI). It appears that neither general tide stage nor time of day have any consistent effect on the average length of time required to catch a fish.

Table V.

Means, standard errors, and number of observations of length of time (hours) between when a male with unfledged young left the nest site with nothing and when he returned with a fish, in each period of the day.

Period	Number of Observations	Mean	Standard Error
05:00-09:00	30	0.5150	0.0884
09:00-13:00	19	0.8860	0.2293
13:00-17:00	36	0.7509	0.1348
17:00-21:00	32	0.4958	0.0705
Overall Mean		0.6426	

Table VI.

Means, standard errors, and number of observations of length of time (hours) between when a male with unfledged young left the nest site with nothing and when he returned with a fish, in each tidal quarter.

Tidal Quarter	Number of Observations	Mean	Standard Error
low to mid-tide	23	0.6906	0.1555
mid to high tide	33	0.6212	0.1064
high to mid-tide	30	0.5983	0.1436
mid to low tide	31	0.6726	0.1184
Overall Mean		0.6426	

Observations of Ospreys with Fledged Young

From 15 June through 19 August 1975, I spent 104.4 hours observing adult ospreys with fledged but dependent young. From 15 through 19 August 1975, I also spent about 15 hours observing fledged and independent young ospreys.

During the 104.4 hours in which I observed ospreys with fledged young, the male ospreys spent an average of 35.29% of the observed daylight hours perched near the nest. Flights where the male flew from the nest area with nothing and returned with a fish occupied 20.86% of the observed daylight hours (N = 17). Flights where the male flew from the nest area with nothing and returned with nothing occupied 27.71% of the observed daylight hours (N = 24). Flights where the male flew from the nest area before I began observing and returned with a fish occupied 6.77% of the observed daylight hours (N = 4). Flights where the male flew from the nest area with nothing and did not return before dusk occupied 5.35% of the observed daylight hours (N = 1). The time use of male ospreys with fledged but dependent young is summarized in Table VII.

During the 104.4 hours in which I observed ospreys with fledged but dependent young, the female ospreys spent an average of 33.83% of the observed daylight hours perched near the nest. Flights where the female flew from the nest area with nothing and

Table VII.

Time use by male and female ospreys with fledged but dependent young based on 104.4 hours of observation between 15 June and 19 August 1975.

		Male		Female	
Behavior		No. Observations	% Time Used	No. Observations	% Time Used
present at or near nest		----	35.29%	----	33.83%
Left					
with nothing	with fish	17	20.86%	29	25.60%
with nothing	with nothing	24	27.71%	16	17.32%
with nothing	with nesting material	4	0.86%	2	0.06%
with fish	with same fish	5	0.46%	3	0.21%
unobserved	with fish	4	6.77%	3	7.37%
unobserved	with nothing	2	2.70%	2	4.79%
with nothing	unobserved (dusk)	1	5.35%	6	10.82%
			100.00%		100.00%

returned with a fish occupied 25.60% of the observed daylight hours (N = 29). Flights where the female flew from the nest area with nothing and returned with nothing occupied 17.32% of the observed daylight hours (N = 16). Flights where the female flew from the nest area before my observations began and returned with a fish occupied 7.37% of the observed daylight hours (N = 3). Flights where the female flew from the nest area with nothing and did not return to the nest area before dusk occupied 10.82% of the observed daylight hours (N = 6). The time use of female ospreys with fledged but dependent young is summarized in Table VII.

When the young were fledged but dependent on their parents for food, the male brought back 39.6% of the fish carried to the nest; the female osprey brought back 60.4% of the fish carried to the nest. The male used an average of 1.28 hours to fly from the nest and return with a fish (17 fish brought to the nest in about 21.8 hours). The male brought fish to the nest at an average rate of 0.2 fish/hour (21 fish brought to the nest in 104.4 observed hours). Females with fledged but dependent young used an average of 0.92 hours to fly from the nest and return with a fish (29 fish brought to the nest in about 26.7 hours). The females brought fish to their nests at an average rate of 0.31 fish/hour (32 fish brought to the nests in 104.4 observed hours). Several transfers of fish from adults to young were observed away from the nest, and young ospreys were seen with fish which they may have

caught themselves. Thus, substantially more fish were fed to the young than were actually brought to the nest when the young were fledged.

There were no significant differences between the percentages of time that the adults (data for males and females combined) were perched at or near the nest in the different 4-hour periods of the daylight hours (analysis of variance, $P > .3636$); the 4 variances were not significantly heterogeneous (Bartlett's test, $.50 > P > .10$; see Table VIII). Apparently, the time of day did not affect the amount of time an adult with fledged but dependent young spent perched near the nest in any consistent manner.

The percentage of time that an adult with fledged but dependent young spent perched near the nest was significantly correlated with the number of young fledged from the nest ($P < .0002$; $\beta = -10.8 \pm 2.02$) and the average relative humidity (%) during the 4-hour period ($P < .0052$; $\beta = 1.05 \pm 0.36$). The bivariate correlation accounted for about 41% of the variation in the percentage of time an adult with fledged but dependent young would spend perched near the nest (coefficient of correlation = 0.413); the number of fledged young alone accounted for over 32% of the variation in the percentage of time an adult would spend perched near the nest (coefficient of correlation = 0.325).

There were significant differences between the rates at which an adult (data for males and females combined) with fledged but

Table VIII.

Means, standard errors, and number of observations of percentages of time that adults with fledged (but dependent) young were perched near the nest in each period of the day.

Period	Number of Observations	Mean	Standard Error
05:00-09:00	8	33.24 %	5.858 %
09:00-13:00	16	30.26 %	8.207 %
13:00-17:00	18	29.17 %	6.764 %
17:00-21:00	18	45.82 %	8.350 %
Overall Mean		35.00 %	

dependent young brought fish to the nest during each of the 4-hour periods of the daylight hours (analysis of variance, $P < .0180$); the 4 variances were not significantly heterogeneous (Bartlett's test, $.50 > P > .10$; see Table IX). The rate at which an adult with fledged young brought fish to the nest during the third period of the daylight hours (13:00-17:00) was significantly greater than the rate at which an adult with fledged young brought fish to the nest during the second and fourth periods of the daylight hours (09:00-13:00 and 17:00-21:00) (Duncan's multiple range test, $P < .05$; see Table X). No other rates were significantly different (Duncan's multiple range test, $P > .05$; see Table X).

The rate at which an adult with fledged but dependent young brought fish to the nest was significantly correlated with the average relative humidity (%) during the 4-hour period ($P < .0161$; $\beta = -0.01 \pm 0.004$) and the average age (days) of the fledged young ($P < .0185$; $\beta = -0.01 \pm 0.004$). That bivariate correlation explained about 15% of the variation in the rate at which an adult brought fish to the nest (coefficient of correlation = 0.15).

Growth and Fledging Weight of Young Ospreys

A total of 27 chicks in 12 broods of ospreys was weighed approximately once every week until the chicks fledged; the results of the weighings are presented in Appendix III. There were 7

Table IX.

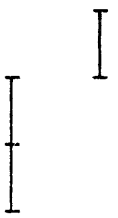
Means, standard errors, and number of observations of rate (fish/hour) at which adult ospreys with fledged (but dependent) young brought fish to their nest in each period of the day.

Period	Number of Observations	Mean	Standard Error
05:00-09:00	8	0.3312	0.0662
09:00-13:00	16	0.1094	0.0455
13:00-17:00	18	0.3611	0.0707
17:00-21:00	18	0.1641	0.0661
Overall Mean		0.2309	

Table X.

Duncan's 5 percent level Multiple Range Test on the rate (fish/hour) at which an adult with fledged young brought fish to the nest in each of the 4 periods of the day.

Period	Mean
13:00-17:00	0.3611
05:00-09:00	0.3312
17:00-21:00	0.1641
09:00-13:00	0.1094



Note: the vertical lines on the right connect mean rates which are not significantly different at P = 0.05.

broods with more than one chick; however, one of those broods (nest 66) was destroyed when the nest was blown or pushed from the supporting duck blind into Harper's Creek. The unexpected result of the weekly weighings of banded chicks was the finding that the "rank" of a chick (its weight relative to its siblings) would often change from weighing to weighing. In 5 of the 6 broods which survived to fledging and which had more than one chick, the relative weights of at least some of the chicks in each nest varied from visit to visit. In nests 56 (2 chicks) and 24 (3 chicks), each chick was at some time the heaviest chick in its nest.

The weight at last weighing prior to fledging of the 25 chicks which fledged, and the size of their brood, are presented in Table XI. The final weights were all taken within about one week of fledging; the single chick in nest 62 was last weighed about 9 days before fledging. There is a significant negative correlation ($P < .0002$; $\beta = -94.7 \pm 20.0$) between the weight (gm) of the chick at its last weighing prior to fledging and the brood size. That is consistent with the fact that the rate at which the male brought fish to the nest did not vary significantly with either the brood size or the average age of the chicks in the nest.

Behavior of Young Ospreys during Feeding

During the first 6 or 7 weeks of the chicks' lives, the male

Table XI.

Brood size and chick weight at last weighing prior to fledging.

Nest Number	Brood Size	Weight at Last Weighing
62	1	1275 gm
04	1	1635 gm
20	1	1715 gm
65	1	1745 gm
57	1	1820 gm
56	2	1680 gm
56	2	1745 gm
35	3	1435 gm
35	3	1525 gm
35	3	1625 gm
24	3	1385 gm
24	3	1405 gm
24	3	1570 gm
17	3	1575 gm
17	3	1605 gm
17	3	1645 gm
38	4	1195 gm
38	4	1245 gm
38	4	1295 gm
38	4	1505 gm
25	5	1220 gm
25	5	1290 gm
25	5	1345 gm
25	5	1370 gm
25	5	1375 gm

brings a fish to the nest, the female usually takes the fish from the male, and the female then feeds the chicks in the chicks in the nest. However, it was not uncommon to see the male feed the chicks on occasion. The feeding adult seemed to feed all chicks in the nest which gaped or called for food. Consistent with that impression is the fact that I never visited a nest and found a chick with an empty crop.

When the chicks are beginning to fledge, the feeding pattern begins to change. The female begins to do a substantial amount of hunting for the chicks (see Table VII), and often when either adult brings a fish to the nest, the fish is simply left at the nest. One of the chicks grabs the fish, and usually eats the entire fish. A hungry chick might call while a sibling was eating, but during 230 hours of observing broods with more than 1 chick, I never saw a chick attack, threaten, or take a fish from an eating sibling.

For about 54 hours, I observed nests with several fledged chicks which usually could be identified by their individual color bands. On 17 July 1975, I observed nest 25 for 8.33 hours; the order in which at least 3 of the 5 chicks in this nest ate was as follows (designating the first chick to eat as 1, the second as 2, and so on): 1, 2, 2, 3, ?, ? ("?" indicates that I was unable to determine the identity of the chick eating the fish). On 18 July 1975, I observed nest 38 for 15.583 hours; the order in which the

4 chicks in this nest ate was as follows: female fed 1, female fed 2 and 3, female fed 4 and 1, 2 took a whole fish, 4 took a whole fish, female fed 1, 3 took a whole fish, 2 took a whole fish, female fed 4, female fed all 4 chicks. On 21 July 1975, I observed nest 35 for 8 hours; the order in which the 3 chicks in this nest ate was as follows: ? took a fish, female fed 1, female fed 2 and 3. On 27 July 1975, I observed nest 38 for 15.5 hours; the order in which the 4 chicks in this nest ate was as follows: 1 took a fish, 2 took a fish, 3 took a fish, 4 took a fish, 1 took a fish, 2 took a fish, 4 took a fish, 3 took a fish, female fed 1, 1 took a fish, 3 took a fish, 2 took fish abandoned by 1, and 4 took fish abandoned by 3. On 10 August 1975, I observed nest 25 for 7.67 hours; the order in which 4 of the 5 chicks in this nest ate was as follows: 1 took a fish, 2 took a fish, 3 took a fish, and 4 took a fish.

Osprey young appear to feed essentially sequentially. On the basis of about 54 hours of observation at those 4 nests, there is no evidence to suggest that one or more chicks dominate the other siblings during feeding. The fluctuations in relative weight of the chicks prior to fledging is consistent with that impression.

Experimental Large Broods

At all osprey nests which I observed, the female ospreys performed the vast majority of the brooding of the chicks. At the

2 nests with experimental large broods, I never saw any evidence that the female was incapable of brooding 5 young; the female seemed capable of keeping the young warm when the temperature was low, and capable of shading them when the temperature was higher. However, at all nests, it was not unusual to see the female in a "shading" posture with panting chick(s) lying in full sunlight.

The 5 chick brood at nest 25 fledged in its entirety; in 51.5 hours of observing this nest, there was never evidence of any sibling incompatability. The 5 chick brood at nest 38 fledged 4 of the 5 chicks; in 61.25 hours of observing this nest, there was also no evidence of any sibling incompatability. The fifth chick in nest 38 died when it was about 10 days old. The carcass was discovered 15 June 1975, removed from the nest, and dissected several hours later. The chick had a large wad of eelgrass (Zostera marina), which is used as lining in osprey nests, in its stomach. Apparently the chick had died of a blockage. There was no evidence such as cuts or bruises to suggest that the chick had died from injuries inflicted from the outside. (On 2 other occasions, I observed osprey chicks eating material lining the nest. On 28 June 1975, I observed the single chick in nest 4 eat a pine needle from the nest; on 18 May 1976, I observed a 3-day old chick on Rigby Island [Milford Haven, Mathews county] eating a piece of eelgrass from its nest).

During the course of this study, 5 other chicks died prior to fledging. No chicks were known to die after fledging. The single

chick in nest 43 was one day old on 31 May 1975; on 7 June 1975, the chick was not in its nest. The 2 chicks in nest 57 were both one day old on 8 June 1975; on 15 June 1975, only one chick was in the nest. The 3 chicks in nest 66 died at about 28, 29, and 31 days of age when their nest was blown or pushed from the supporting duckblind. Since 2 other chicks in smaller broods also died during this study, the death of the chick in nest 38 is not unusual enough to implicate the large brood size as a factor in the chick's death. The successful fledging of all 5 chicks from nest 25 is consistent with that conslusion.

It seems there is no evidence from this study to suggest that 5 chicks could not successfully cohabit a single nest.

Familial Longevity

I observed 11 nest sites in 1975 after the chicks had fledged. The chicks in a particular family unit were identified by the unique combinations of aluminum and color bands on their legs; the adults in a particular family unit were identified by certain behaviors (e.g., feeding a color-banded chick, or perching at a particular nest site).

The chicks at the 11 nests observed here fledged when they were 44-59 days old (mean = 51 days); brood size did not seem to influence the age at which fledging occurred. Not all family units centered their activities in the vicinity of the nest site

after the chick(s) had fledged. At nest 24, the family unit was observed to be intact, but had moved from the vicinity of the nest within 2 days of the chicks' fledging. At 2 nests (4 and 62), the family unit apparently left the vicinity of the nest within 10 days of the chicks' fledging. At nest 65, the family unit was intact at the nest site when the single chick was 78 days old, but 4 days later the family unit was not observed in the area again.

The family units at other nests were intact in the vicinity of their nest sites at least until the time when the chicks were 65-93 days old. At nest 35, the chicks were fed by their parents at least until they were 75-79 days old. At nest 65, the single chick was being fed by its parents when it was 78 days old. At nest 25, the chicks were being fed by their parents at least until they were 80-89 days old. But at nest 16, the adults were absent from the area and the 2 chicks were catching their own fish when the chicks were about 103 days old; the chicks were active in the vicinity of their nest at least until they were 108 days old, at which time my observations terminated.

DISCUSSION

Lack's Hypothesis

David Lack (1954, 1966, and elsewhere) has argued that birds with nidicolous young lay a clutch which corresponds to the largest number of healthy young which usually can be adequately fed. Lack (1970, p. xiii) states the hypothesis as follows: "In those birds which feed their young, the reproductive limit - the clutch-size - has been evolved through natural selection in relation to the maximum number of young for which the parents can provide enough food without detriment to themselves." Ospreys usually lay clutches of 3, and occasionally 2 or 4, eggs (Bent 1937, p. 360). Jones (1936) reported a mean clutch size of 2.91 eggs for 11 nests with eggs in southeastern Virginia. In apparent contradiction to Lack's hypothesis, the male ospreys with unfledged young which I observed in 1975 spent a major portion (42.66%) of the daylight hours perched near the nest. Since the male does essentially all of the hunting for the family unit until the chicks are fledged, it would seem that if a male hunted more, he would be able to feed adequately a larger number of healthy young in each brood.

Factors which could conceivably limit the number of healthy young which can be successfully reared must be considered over all stages of the breeding cycle if Lack's hypothesis is to be rigorously tested. It appears that ospreys return from the wintering grounds to the breeding grounds separately. Either the female (e.g., Latham 1928) or the male (e.g., Bent 1937, p. 353; Kennedy 1971) of the pair will return to the breeding grounds first; the other member of the pair usually arrives at the area within several days. Even though there is some suggestion that ospreys mate for life (Bent 1937, p. 354), there is no evidence that the pair winters together on the South American wintering grounds. The fact that the pair returns to the breeding grounds separately suggests that they do not winter together. Consequently, there would seem to be no familial requirements affecting ospreys before their return to the breeding grounds.

Moss, Watson, and Parr (1975) have shown that maternal nutrition during egg-formation can affect breeding success in the red grouse (Lagopus lagopus). It is certainly conceivable that maternal nutrition on the wintering grounds could significantly affect the breeding success of ospreys. However, based on studies of other avian species, one would estimate that the time required for the rapid phase growth of the follicles (which immediately preceeds egg-laying) of a female osprey would be about 10 days (Ricklefs 1974, figure 3). Since ospreys usually return to the

breeding grounds a month or more before egg-laying occurs, it seems unlikely that maternal nutrition on the wintering ground will seriously limit egg production on the breeding grounds. Thus, there is no evidence that earlier social or nutritional events on the wintering grounds (excluding death or injury of an adult) will significantly affect the number of healthy young which can be reared successfully.

Although there are several reports indicating that the osprey family unit remains intact for at least several days after the chicks fledge (e.g., Bent 1937, p. 364; Meinertzhagen 1954; Stinson 1976), the only published report dealing with the duration of the osprey family unit seems to be Beebe's (1974, p. 41) comment that there is a post-fledging association of the young and the adults which may possibly last up to 60 days after fledging occurs. Since the parents expend energy for the fledglings until the family unit is dissolved, determination of the length of time the osprey family unit remains intact is important in understanding osprey reproductive ecology. If the family unit remained intact during migration and on the wintering grounds in South America, the energy and time "invested" in the fledglings by the parents would be much greater than if the family unit separated before migration; evaluations of whether or not the parents were performing optimally, as predicted by Lack, would have to be revised accordingly.

Stotts and Henny's (1975) report that ospreys at 18 nests fledged at 48-59 days of age (mean = 54 days) is similar to my

observation that the chicks at 11 nests in this study fledged at 44-59 days of age (mean = 51 days). The slightly different mean fledging age of my observations and those of Stotts and Henny (1975) is possibly due to my visiting the nests slightly more frequently than Stotts and Henny did. If my further observations on osprey familial longevity at the 4 nests mentioned earlier are indicative of ospreys in general, the osprey family unit is intact until the chicks are about 93-103 days old. Apparently, the osprey family unit breaks up before the fall migration to the wintering grounds begins. That conclusion is consistent with both Beebe's (1974, p. 41) comment, and with the fact that migrating ospreys are usually seen alone or in pairs (Brown and Amadon 1968, p. 198). Therefore, I consider the significant stages of the breeding cycle of the osprey to encompass the earliest days that the adults are together on the breeding grounds through the last days that the family unit (adults, and the fledglings still dependent on the adults for food) is together as a group. Knowledge of the parents' performance during the summer apparently should be adequate to evaluate whether or not ospreys achieve the maximum reproductive effort predicted by Lack.

Assuming that knowledge of the parents' performance on the breeding grounds is sufficient to evaluate Lack's hypothesis, I have formulated 7 hypotheses which allow the male's spending substantial amounts of time perched near the nest to be interpreted

in such a manner that it is consistent with Lack's hypothesis; they are presented below.

(1) In the years since the development and application of chlorinated hydrocarbon pesticides, ospreys have become much less abundant in many areas (for a review of the literature, see Via 1975). Perhaps, since ospreys were once more abundant, intra-specific competition for food was once much more pronounced, and 3, or occasionally 4, young was the largest number of healthy young which usually could be fed adequately.

(2) Perhaps the male must spend a major portion of the day perched near the nest to guard the chicks from potential predators. Consequently, the brood size is limited to the number of chicks which can be both fed and guarded; the male appears to be "wasting" time when he is, in reality, performing an essential task. Slack (1976) has demonstrated such nest-guarding behavior by the male grey catbird (Dumatella carolinensis).

(3) Perhaps the male cannot hunt, or cannot hunt as efficiently, during periods of inclement weather (e.g., rainy, windy, and/or overcast conditions). Consequently, the brood size would be limited to the number of chicks which could be fed during inclement weather, and the male would appear to be "wasting" time during balmy weather.

(4) Perhaps the male avoids hunting during the hotter parts of the day to avoid heat stress; both this hypothesis, and the 2

following, incorporate Lack's suggestion (1970, p. xiii) that the adults feed the largest number of young possible "without detriment to themselves". Ricklefs (1971) has argued that heat stress (or, the possibility of heat stress) limits the amount of time available for hunting for mangrove swallows (Iridoprocne albilinea). Consequently, the brood size would be limited to the number of young which could be fed during hotter weather, and the male would appear to be "wasting" time during hot weather.

(5) Perhaps the male must rest for a substantial portion of each day due to fatigue incurred during foraging.

(6) Perhaps the production of more than 3, or occasionally 4, eggs by the female osprey requires more energy than is usually available at the time the female is producing the eggs; for most birds, egg-production by the female requires substantial amounts of energy (Ricklefs 1974). Regardless of how much time the male is "wasting", his behavior is still consistent with Lack's hypothesis if the female osprey usually cannot obtain the energy to produce more than 3, or occasionally 4, eggs.

(7) Perhaps after the chicks fledge, hunting conditions are so unfavorable that 3, or occasionally 4, young is the largest group of young which the 2 parents can adequately feed, even though the male could feed more chicks before then fledge. Thus, the male appears to be "wasting" time because although he could feed more unfledged chicks, it is usually impossible for the male and female together to feed more chicks after they fledge.

The first hypothesis considered here is that intra-specific competition for food was once much greater because the Virginia osprey population was once much larger, and consequently, at one time the number of chicks which could be successfully fledged was limited by intra-specific competition for food. Osprey breeding populations in Virginia were probably once about 5 times larger than they currently are (Stinson and Byrd 1976). If one considers a fish population of n individuals which is being fished by ospreys which remove m fish per osprey, and if n is much, much larger than m (as is undoubtedly the case for ospreys in the Chesapeake Bay estuarine system), then the number of fish available to a present-day osprey hunting over the fish population (n) is about equal to the number of fish available to an osprey in the past hunting over a fish population that 4 other ospreys have fed from ($n - 4m$). Thus, even though earlier osprey populations were probably somewhat larger than they are now, it seems doubtful that there were ever so many ospreys that intra-specific competition for food was limiting the number of healthy young which could be reared. Additionally, MacCarter (1972), Ueoka (1974), and Swenson (1975) all conclude that food was probably not a limiting factor for the osprey populations they studied.

Schmid (1966, p. 222) in his discussion of New Jersey osprey populations remarks that the "disappearance of pound nets undoubtedly has made it harder for ospreys to find food in many

areas", implying that ospreys obtain a substantial portion of their food from those permanent fishing nets. However, it is my observation that ospreys rarely take fish from pound nets; the overwhelming majority of the fish which ospreys catch seem to be taken "wild". It seems unlikely that the presence or absence of pound nets significantly affects the food available to an osprey population.

Charnov, Orians, and Hyatt (1976) have pointed out that when studying prey availability, it is ususlly not enough to consider only prey numbers as I have done above; they are specifically concerned with "resource depression", i.e., behavioral responses of prey to the presence of predators which make the prey less available than mere numbers would suggest. However, since the majority of fish predators are other fish (e.g., Charnov, Orians, and Hyatt 1976; Zaret and Paine 1973), it does not seem likely that piscivorous birds will often be affected by resource depression (Charnov, Orians, and Hyatt 1976). Thus, it is probably sufficient to consider only numbers of prey as a measure of prey availability for ospreys. I conclude that it is extremely doubtful that intra-specific competition for food was once a factor limiting the number of young ospreys which a pair of ospreys could adequately feed. The fact that ospreys do not have defended hunting territories (unlike many other raptors) (Swenson 1975; personal observation) and that they often nest in large aggregations (e.g., Allen 1892;

Bailey 1876; Chapman 1908; Hallock 1897; Jones 1936; Wilcox 1932) is consistent with that conclusion.

The second hypothesis which might explain the male's behavior in a manner consistent with Lack's hypothesis is that the male must spend a substantial portion of the day guarding the family unit at the nest. The major difficulty with accepting this hypothesis is that ospreys have relatively few predators. Lafontaine and Fowler (1976) reported a golden eagle (Aquila chrysaetos) killing an osprey. Reese (1970) reported a great horned owl (Bubo virginianus) possibly preying on unfledged ospreys. Bent (1937, pp. 372-373) reported several magnificant frigatebirds (Fregata magnificans) killing an osprey and mentioned what might have been fish crow (Corvus ossifragus) predation on osprey eggs. Allen (1892) also mentions fish crow predation on osprey eggs. But, in general, reports of predation on ospreys are rare. Additionally, the female osprey (who is with the unfledged chicks about 95% of the daylight hours; Table I) is generally the more aggressive of the pair (Bent 1937, p. 369; personal observation) and is more likely to attack potential predators than is the male.

Ogden (1975) reports that ospreys in Florida can suffer reduced nesting success when nesting near bald eagles (Haliaeetus leucocephalus), but that phenomenon is limited to the first year of the association; after the first year of nesting near each other, the birds apparently acclimate to each other's presence

and normal osprey nesting success resumes. That situation is unlikely to affect ospreys nesting outside of Florida, however, for elsewhere ospreys and bald eagles usually do not nest at the same time of year (e.g., Beebe 1974, p. 40). Bald eagles are also known to pursue ospreys carrying fish in an attempt to steal the fish (e.g., Bent 1937, pp. 371-372), but ospreys are apparently just as likely to harass bald eagles (Bent 1937, p. 372; Garber 1972; Swenson 1975) and the phenomenon would not account for the male guarding the nest area. There are also 2 reports of gulls (Larus spp.) unsuccessfully attempting to take fish from ospreys (Ransom 1932; Leck 1973) and I have observed laughing gulls (Larus atricilla) do the same; however, gull harassment probably has a negligible effect on ospreys and, again, would not account for the male guarding the family unit.

The fact that ospreys have so few potential predators, and that the female osprey is more likely to be the adult which will attack any predator, suggests that the male does not perform an essential guarding function at the nest. Thus, I reject the hypothesis that the male must spend a substantial portion of the day guarding the family unit at the nest.

A third interpretation of the male's behavior that would be consistent with Lack's hypothesis is that the male osprey is a less efficient hunter during periods of inclement weather.

Presumably, the male must hunt a greater proportion of the time during inclement weather than during balmy weather because he is less efficient at capturing fish during inclement weather. The male would appear to be "wasting" time during balmy weather because the brood size is limited by the food he can supply during inclement weather. If the above hypothesis were true, one would expect a strong correlation between some environmental factor(s) and the rate at which fish were brought to the nest by the hunting male; one would also expect that the average length of time required to catch a fish would be strongly influenced by some environmental variable(s).

Significantly more fish were brought to the nest in the first period of the day (05:00-09:00) than in any other 4-hour period of the day. Since there was no significant difference in the mean length of time required to catch fish in the different sections of the day, that result cannot be interpreted to mean that fish were more difficult to catch later in the day. Probably ospreys were hungrier in the early morning (after not eating all night) than at other times of the day. Ueoka (1974) found that osprey foraging in Humboldt Bay, California, was concentrated in the hours immediately after the morning fog lifted from the bay.

Ueoka (1974, pp. 53-54) suggests that "mean length of time actually spent foraging is a better indicator of relative difficulty in locating prey" than is the "average time providing-parents were absent from their nests". At least for ospreys in

Humboldt Bay, the former was only about one-sixth the time of the latter, since after capturing a fish the hunting adult would usually land away from the nest and eat part of the fish before returning to the nest (Ueoka 1974). However, for the purpose of determining whether or not the male osprey is feeding the maximum possible number of young, the "average time providing-parents were absent from their nests" seems to be a better indicator of the difficulty of bringing prey to the nest, for it includes not only the time actually spent foraging, but also the time the male must spend obtaining his own nourishment.

The length (hr) of flights when the male flew from the nest area with nothing and then returned with a fish was correlated significantly with the average difference between the maximum and minimum wind speeds (miles/hour) recorded every quarter-hour ($P < .0002$; $\beta = 0.08$), the average age (days) of the chicks in the nest ($P < .0002$; $\beta = 0.03$), the number of eggs in the nest ($P < .0130$; $\beta = 0.55$), and the number of chicks in the nest ($P < .0230$; $\beta = 0.09$). Neither tide stage nor time of day significantly changed the length of hunting trips.

The apparent contradiction of the positive correlation of hunting time with both the average age of the chicks and the number of eggs in the nest (which decreased as the average age of the brood increased, because the eggs eventually hatched), is probably due to the male's attentiveness at the nest site increasing sharply as the chicks begin to hatch and declining

slowly as they age. Consistent with that interpretation is that the rate at which fish were brought to the nest did not change as the chicks aged, and only the average age of the chicks in the nest was significantly correlated with the percentage of time the male spent perched near the nest ($P < .0002$; $\beta = -1.0$). The positive correlation of hunting time with the number of chicks is possibly due to the attentiveness of males with large broods declining faster than that of males with small broods. Consistent with that is that there was no correlation between the rate at which the male brought fish to the nest and the number of young in the nest. The total correlation accounted for about 32% of the variation in hunting time; the average difference between the maximum and minimum wind speeds accounted for about 16.5% of the variation in hunting time.

The rate at which the male brought fish to the nest (fish/hour) was significantly correlated with the average rate of precipitation (mm/.25 hr) ($P < .0036$; $\beta = -0.6$), the average dry-bulb temperature (^{o}C) ($P < .0159$; $\beta = -0.3$), the average "modal" wind speed (miles/hour) ($P < .0129$; $\beta = 0.05$), and the maximum wind speed (miles/hour) ($P < .0218$; $\beta = -0.03$). Although these environmental factors had a significant effect on the rate at which the male brought fish to the nest, they accounted for only 16% of the variation in the rate at which the male brought fish to the nest. Each independent variable alone accounted for about 4% of the

variation in the rate at which the male brought fish to the nest. More importantly, the percentage of time that the male was perched near the nest was not significantly correlated with any of those variables, implying that the male hunted neither more nor less during periods of rain and high winds. Although both the length of hunting trips and the rate at which the male brought fish to the nest are affected by inclement weather (i.e., rain and high winds), inclement weather does not seem to account for the male spending a substantial portion of each day perched near the nest.

The rate at which the male with unfledged young brings fish to the nest is lowest during periods of inclement weather (i.e., during periods of rain and high winds). The largest number of young which the male can feed adequately is probably limited to the number which can be fed adequately during periods of inclement weather. However, the male apparently manages to feed 3, and occasionally 4, young adequately during periods of inclement weather despite the fact that the male spends over 40% of the time perched near the nest. It would appear that if the male hunted more during periods of inclement weather, a larger brood could be fed adequately. That is, while the maximum number of young which can be fed adequately is probably limited primarily by periods of inclement weather, during periods of inclement weather the male does not appear to be utilizing the time available for hunting to its fullest. Thus, I reject the hypothesis that the brood size of

ospreys is limited to 3, or occasionally 4, young because the male would be unable to feed a larger brood adequately during periods of inclement weather.

The fourth hypothesis which would explain the male's behavior (perching near the nest for a substantial portion of each day) in a manner consistent with Lack's hypothesis is that the male osprey does not hunt, or does not hunt as often, during periods of hot weather due to the possibility of heat stress. If that hypothesis were true, one would expect a significant positive correlation between the percentage of time in each period of the day that the male was perched near the nest and relative humidity, temperature, and sunniness. None of those environmental parameters were significantly correlated with the percentage of time that the male was perched near the nest in each section of the day. Thus, I reject the hypothesis that the male osprey does not hunt, or does not as often, during periods of hot weather due to the possibility of heat stress.

Spotila and Gates (1975, figure 17.1) calculate that for an average homeotherm with a body temperature of 42 ^{o}C, a body diameter of 10 cm, and an insulative layer (i.e., fur or feathers) which is 10% of the body diameter (parameters which roughly approximate the body temperature and dimensions of an adult osprey), to maintain thermoneutrality in an environment with an ambient temperature of 40 ^{o}C (a temperature higher than any which I recorded in the field),

the heat lost by evaporative water loss must exceed the heat generated metabolically by a minimum of 0.05 cal cm^{-2} min^{-1}.

Calder and King (1974, p. 271) suggest that the standard metabolic rate of an active (i.e., non-sleeping) nonpasserine can be estimated from the bird's body weight by the allometric equation,

$$SMR = 91.0\ M^{0.729}, \qquad (1)$$

where SMR is the standard metabolic rate in kcal/day, and M is the body weight in kg. Since the body weight of an adult male osprey is about 1403 gm (Brown and Amadon 1968, p. 195), the standard metabolic rate of an adult male osprey would be estimated to be 116.5 kcal/day, or about 80.9 cal/min. The metabolic rate of a nonpasserine in flight is about 10 times the bird's standard metabolic rate (Calder and King 1974, p. 312). Thus, the metabolic heat production of an adult male osprey in flight would be estimated to be about 809 cal/min. The surface area of a bird can be estimated from its body weight by the allometric equation,

$$A = 10\ m^{0.67}, \qquad (2)$$

where A is the surface area in cm^2, and m is the body weight of the bird in gm (Calder and King 1974, p. 275). The surface area of an adult male osprey would be estimated to be about 1284 cm^2; the metabolic heat production per unit area of an adult male osprey in flight would be estimated to be about 0.63 cal cm^{-2} min^{-1}.

The heat lost by evaporative water loss can be estimated from the allometric equation derived by Berger and Hart (1974, p. 453),

$$C = (0.8\ M)/[W^{2/3}(T_b - T_a)]\ \text{cal gm}^{-2/3}\ \text{min}^{-1}, \qquad (3)$$

where $\underline{M}$ is the metabolic rate in cal/min, $\underline{W}$ is the body weight of the flying bird in gm, and $\underline{T}_b$ and $\underline{T}_a$ are the body temperature and the ambient temperature (^{o}C) respectively. To convert equation 3 into units of cal cm^{-2} min^{-1}, body weight is converted to surface area by equation 2. Thus, the heat loss due to evaporative water loss by a flying bird is,

$$C = (8\ M)/[A\ (T_b - T_a)]\ \ \text{cal cm}^{-2}\ \text{min}^{-1}. \qquad (4)$$

Using the previously derived values for metabolic rate and surface area, and the previously defined temperatures for body temperature and ambient temperature, the heat loss due to evaporative water loss by a flying male osprey is estimated to be about 4.37 cal cm^{-2} min^{-1}.

Osprey-like homeotherms are theoretically required to have a rate of evaporative heat loss which is 0.05 cal cm^{-2} min^{-1} greater than their rate of metabolic heat production. 4.37 cal cm^{-2} min^{-1} is 3.74 cal cm^{-2} min^{-1} greater than 0.63 cal cm^{-2} min^{-1}, certainly well above the critical minimum difference. Thus, if one is willing to accept these estimations based on data from other avian species, one would not expect adult male ospreys to suffer from heat stress at 40 ^{o}C. In light of that, the field observations

suggesting that male ospreys do not avoid hunting during the hotter parts of the day do not seem surprising.

The fifth hypothesis which would explain the male's spending a substantial amount of time perched near the nest in a manner consistent with Lack's hypothesis is that the male must rest for a substantial portion of the day due to fatigue incurred during foraging. Indeed, the duration of hunting theoretically could be limited not only by the bird's ability to dissipate heat (heat stress), but also by limits to energy mobilization or by the work potential of the bird's muscles (Ricklefs 1974). However, Berger and Hart (1974) suggest that for birds in general, the maximum length of flights is limited in fact only by a bird's energy reserves, implying that speed of energy mobilization and the work potential of the muscles are unlikely to be factors limiting the duration of foraging effort. It seems that the only fatigue at all likely to be incurred by a foraging osprey would be due to heat stress. I have already rejected the hypothesis that osprey foraging time is limited by the possibility of heat stress, and consequently, I reject the hypothesis that the male must rest for a substantial portion of each day due to general fatigue incurred while foraging.

The sixth hypothesis which attempts to interpret the behavior of the male osprey in a manner consistent with Lack's hypothesis is that the female osprey usually cannot obtain the energy to produce more than 3, or occasionally 4, eggs. For most birds, egg production by the female is a process which requires substantial

amounts of energy (Ricklefs 1974). However, Ricklefs (1974) also points out that birds such as most raptors (including ospreys), which generally lay one egg every other day until the clutch is complete, are the exception to the rule that egg production is a tremendous energetic stress on the female. While the energy requirement for laying the complete clutch is over 100% of the basal metabolic rate (BMR) for most birds, for raptors the energy requirement is only about 39% of the BMR (Ricklefs 1974, Table 12). Consequently, one would not expect that an inordinate amount of food would be required to feed an egg-producing female osprey. If food were especially difficult to catch at the time of year when the female was producing eggs, it would not matter how relatively little the female required if that "relatively little" was not easily available in the environment. However, if my observations on ospreys' hunting behavior prior to egg-laying are indicative of the situation in general, fish are no more difficult to catch early in the season than they are at any other time. Ueoka (1974) also found that osprey hunting trips were shortest during the pre-incubation period. Thus, there seems to be no energetic reason that the female could not produce a larger clutch, and thus, I reject the hypothesis suggesting that the female usually cannot obtain enough energy to produce more than 3, or occasionally 4, eggs. Chapman's (1908) comment that, for the osprey population on Plum Island, New York, food seemed abundant prior

to egg-laying is consistent with the rejection of that hypothesis (Plum Island ospreys also usually laid clutches of 3 eggs).

The seventh hypothesis which interprets the behavior of the male osprey with unfledged young in a manner consistent with Lack's hypothesis is that hunting conditions are so unfavorable after the young fledge, that 3, or occasionally 4, young are the most which the 2 parents can adequately feed. The average length of each hunting trip for a male with fledged but dependent young was 1.28 hours/fish, and the average length of each hunting trip for a female with fledged but dependent young was 0.92 hours/fish. The average length of each hunting trip for a male with unfledged young was 0.64 hours/fish. Hunting trips of adults with fledged but dependent young are longer than hunting trips of males with unfledged young. It is not immediately apparent whether that difference is due to males with unfledged young being generally more attentive at the nest site than adults with fledged young, or whether that difference is due to a deterioration of hunting conditions after the chicks fledge. Additionally, the rate at which the 2 adults with fledged young brought fish to the nest was about equal to the rate at which the male alone brought fish to the unfledged young (0.510 fish/hour as opposed to 0.516 fish/hour). It is not immediately apparent whether that is because the 2 adults cannot bring more fish to the nest, or whether that is because they do not need to bring more fish to the nest.

The percentage of time which an adult with fledged but dependent young spent perched near the nest in each section of the day was correlated with both the number of chicks in the brood ($P < .0002$; $\beta = -10.8$) and the relative humidity (%) ($P < .0052$; $\beta = 1.05$). The bivariate correlation accounted for about 41% of the variation in the percentage of time an adult would spend perched near the nest in each period of the day; variation in relative humidity accounted for less than 9% of the total variation in the percentage of time an adult would spend perched near the nest each period of the day. The rate at which an adult with fledged but dependent young brought fish to the nest was correlated with both the average age (days) of the young ($P < .0161$; $\beta = -0.01$) and the relative humidity (%) during the 4-hour period ($P < .0185$; $\beta = -0.01$). Variation in the 2 independent variables accounted for 15% of the variation in the rate at which an adult brought fish to the nest during each period of the day, with each independent variable explaining approximately equal portions of the variation. Relative humidity has a significant effect on the percentage of time an adult is perched near the nest and on the rate at which fish are brought to the nest by the adults. However, the effect is small as can be seen by examining the amount of variation which is explained by relative humidity (less than 10% in both cases). Thus, although relative humidity affects the hunting behavior of the adults, it does not appear to be limiting the number of fledged young which can be fed adequately to 3 or 4 young.

Additionally, as a general rule, the energy requirements of young birds are higher just prior to fledging than they are after fledging. Before fledging, the young have energy requirements due to growth and maintenance, while after fledging, very little growth occurs and energy demands are primarily due to maintenance (Ricklefs 1974). If fish were much more difficult to catch at the time of year when the young have fledged, even though both parents were bringing substantial amounts of food to the nest, and even though the energy requirements of the fledged young are probably less than they were before fledging, the hypothesis that hunting conditions deteriorate about the time the young fledge could be accepted.

The dates at which young fledged from the nests ranged from before 15 June to after 4 August 1975. Yet, hunting adults with fledged young tended to stay away from the nest longer than hunting adults with unfledged young regardless of date of fledging. Since the fledgings did not occur simulatneously, but the adults' behavior changed when the young fledged, it seems unlikely that the increased length of hunting trips is due to deterioration of hunting conditions at fledging time. The increased length of hunting trips is probably due to decreasing attentiveness at the nest sites on the part of the parents. Since fish do not seem to be substantially more difficult to capture after fledging occurs, I reject the hypothesis that hunting conditions after the young fledge are so unfavorable that 3, or occasionally 4, young are the most which the 2 parents can adequately feed.

There seems to be no explanation which is consistent with both Lack's hypothesis and my observations, of the fact that male ospreys with unfledged young spend substantial portions of each day perched near the nest. Lack's hypothesis is undoubtedly true for the majority of nidicolous bird species which have been studied (e.g., Lack 1966), but it does not appear to be universally true for all nidicolous birds (e.g., ospreys). Consequently, I reject Lack's hypothesis that all birds with nidicolous young lay a clutch which corresponds to the largest number of healthy young which usually can be fed.

Traditional Alternatives to Lack's Hypothesis

It appears that some other factor or factors have influenced the evolution of the clutch-size of the osprey. Stearns (1976) and Klomp (1970) discuss the alternative hypotheses regarding the evolution of brood size. Several of the hypotheses mentioned by Stearns (1976) are modifications of Lack's hypothesis and will be discussed later. However, there are 5 hypotheses which are inconsistent with Lack's hypothesis and they are discussed here: (1) all female ospreys are physiologically incapable of producing more than 3, or occasionally 4, eggs; (2) all ospreys are incapable of successfully incubating more than 3, or occasionally 4, eggs; (3) all ospreys are incapable of successfully brooding more than 3, or occasionally 4, young; (4) due to sibling intolerance and

interference, it is impossible for more than 3, or occasionally 4, young ospreys to cohabit a nest successfully; and (5) reproductive effort in ospreys has evolved by group selection, and ospreys are producing only as many young as are needed to balance population mortality.

With regard to the first hypothesis, there are at least 3 records of clutches of 5 osprey eggs (Allen 1892; Bailey 1913, p. 129; Bent 1937, p. 360) and there are at least 2 records of broods of ospreys with more than 4 young (Aldrich 1888; Howe 1895). About 12% of the ospreys currently breeding in Virginia lay 4 egg clutches (Mitchell A. Byrd, personal communication) suggesting that more than an "occasional" osprey is capable of laying 4 eggs. Also possibly of significance here, female ospreys are capable of re-laying a second clutch if their first clutch disappears (Kennedy 1971). If it were impossible for all female ospreys to lay a clutch of 4 or 5 eggs, there would be no way that trait could be selected for. Lack's hypothesis is based in part on the assumption that the birds in question are capable of laying an "optimum" number of eggs (and incubating the "optimum" clutch, and brooding the maximum number of young which can be fed adequately, etc.). Since it is possible for some female ospreys to lay 5 egg clutches, and for many female ospreys to lay 4 egg clutches, a larger clutch size could be selected for. Thus, I reject the hypothesis that female ospreys are physiologically

incapable of producing more than 3, or occasionally 4, eggs.

With regard to the second hypothesis, the fact that the brood of 5 ospreys mentioned by Aldrich (1888) and the brood of 7 ospreys mentioned by Howe (1895) both hatched suggests that at least some ospreys are capable of successfully incubating more than 3, or occasionally 4, eggs. Thus, I also reject the second hypothesis that all ospreys are incapable of successfully incubating more than 3, or occasionally 4, eggs. That is consistent with Klomp's (1970) statement that inability to incubate successfully a larger clutch is unlikely to be a factor limiting the clutch size of birds.

The fact that one of the 5 chick broods fledged successfully indicates that ospreys are capable of brooding more than 3, or occasionally 4, young. The success of 4 chick broods in general indicates that this hypothesis is inadequate to explain why ospreys usually have clutches of only 3 eggs. That is, even if osprey fledging success was limited only by the inability of ospreys to brood more than 3, or occasionally 4, young, natural selection would still select for ospreys laying 4 eggs (since occasionally even the fourth chick would fledge). Thus, I reject the hypothesis that ospreys are incapable of successfully brooding more than 3, or occasionally 4, young. My observations of brooding ospreys are consistent with that rejection.

The fourth hypothesis is that due to sibling intolerance or interference, it is impossible for more than 3, or occasionally 4,

young ospreys to cohabit a nest successfully. The most destructive form of sibling interference is cainism, where one raptor kills its sibling(s). Ospreys, however, apparently do not engage in cainism. Brown (1970), while mentioning other species of raptors for which the "Cain and Abel battle" has been observed, does not mention that it has been observed for ospreys. Olendorff (1971) in his extensive review of the raptorial literature does not mention any observations of osprey chicks attacking or killing a sibling, although he does cite reports of other species behaving in such a manner. There is no suggestion that ospreys engage in cainism in the discussions of the natural history of the osprey by Bent (1937) or Brown and Amadon (1968). Consistent with the above evidence is that during almost 300 hours of observing osprey nests which contained unfledged chicks in 1974 and 1975, I never saw any sibling interactions which suggested that a chick was being harmed in any way by a sibling. In 259 hours of observing 2 ospreys nests with unfledged young, Ames (1964) also did not record any attacks on a chick by a sibling. Chicks from one of the 2 experimental broods of 5 chicks all fledged successfully, and 1 chick in the second brood of 5 died, but apparently not of any external injury. Thus, although it is always difficult to determine that an event does <u>not</u> occur, cainism does not appear to be a factor significantly affecting the survival of young ospreys.

Further, it seems unlikely that any behavioral dominance

between siblings limits the number of osprey chicks which can cohabit a single nest successfully. Successful broods of 4 young ospreys are unusual only because a 4 egg clutch is relatively uncommon; cohabitation of a single nest by 4 young seems to present no serious problems. Feeding is not dominated by one or a few chicks, but is essentially a sequential event, both unfledged and fledged young being fed "in turn". This further suggests that there is little, if any, significant behavioral dominance. Ames' (1964, p. 22) observations of unfledged ospreys being fed are consistent with mine: "The feeding of young birds of prey is often pictured as a strongly competitive process, with the weakest nestling being fed last. In many cases [involving other species of raptors] that is certainly true, but in our [osprey] nest with the three young it was far from the case." Green (1974, p. 29) also comments that although "in many raptor species there is fighting between the chicks for food and the youngest often starves, this does not seem to be the case with osprey chicks, relations between which appear to be very peaceful." The fact that the ranked weights of the young in a nest can vary from week to week (Garber 1972; Appendix III) also supports the idea that there is little, if any, detrimental effect on one sibling from other siblings in the nest. Thus, I reject the hypothesis that sibling interference or intolerance plays a major part in the success or failure of large osprey broods, and consequently, I assume that it does not limit osprey reproductive effort.

The fifth hypothesis which could explain the observed clutch size of ospreys is that group selection, and not individual selection, has acted to limit individual reproductive effort (Wynne-Edwards 1962, 1964; Skutch 1967). Two viable models of group selection have been proposed (Gilpin 1975; D.S. Wilson 1975), but both of those models have assumptions or structures which are not consistent with osprey population biology. Gilpin's model assumes that the predator preys on only one prey species; however, ospreys feed on many species of fish (e.g., Bent 1937, p. 366). Wilson's model relies on the existence of "trait-groups", a sub-demic assemblage which does not seem to have a counterpart in osprey populations. Thus, although it is conceivable that osprey reproductive output could be limited by some form of group selection, there are currently no known processes by which group selection could act on osprey populations to limit individual reproductive output. Consequently, I reject all attempts to explain the pattern of osprey reproduction as a product of group selection because there is no known mechanism by which it could have evolved.

Modifications of Lack's Hypothesis

Stearns (1976, pp. 17-18) in his review of life history theory discusses "five theoretical models" which "incorporate mechanisms

that account for the reduction of clutch size below the most productive size: (1) trade-offs between demands for resources on the part of reproductive versus other functions (Cody, 1966; Skutch, 1967); (2) trade-offs between clutch size and adult mortality (Charnov and Krebs, 1973); (3) bet-hedging in the face of uncertainty about conditions during the breeding season (Boer, 1968; Holgate, 1967); (4) the interaction of a normal distribution of clutch sizes with a probability of recruitment that declines with increasing clutch size (Mountford, 1968); and (5) a positive correlation between clutch size and the probability of extinction where the population is broken up into groups of closely related organisms (Gilbert and Gutierrez, 1973)." Stearns regards these models as modifications of Lack's hypothesis. While that is questionable for some of the above hypotheses (e.g., Mountford 1968), all of them will be considered here.

The hypothesis of Skutch (1967, and elsewhere) and Cody (1966) is that organisms have a finite amount of resources (e.g., time and energy) available, and those resources must be used for predator avoidance, competition, and reproduction. That is, not all of an organism's time can be devoted to reproductive effort. As argued previously, ospreys have very few potential predators, so it seems unlikely that the male osprey spends a substantial amount of time perched near the nest in an attempt to avoid predators. Ospreys do not defend their hunting territories, and

so do not have a substantial time or energy requirement due to territorial competition or defense. Additionally, a time requirement due to competition would not explain why the male spent a substantial amount of time perched near the nest. Thus, I reject the hypothesis that the male osprey with unfledged young spends a substantial portion of each day perched near the nest due to the competing time demands of predator avoidance, intra-specific competition, and reproductive efforts.

The second hypothesis considered in this section is that ospreys are not rearing the largest brood they possibly could because there is a trade-off between clutch size and adult mortality involved. Williams (1966, p. 245) made this argument when he said "that some species, such as eagles, have low intensities of reproductive effort because of a low probability of death from one breeding season to the next." Presumably, a more intense reproductive effort (i.e., a larger clutch and brood) would increase the probability of death for the adult and would shorten the average adult life-span drastically; thus, even though the annual reproductive effort would be more intense, the decrease in average life-span would be so great that the individual would leave fewer young than a longer-lived individual with a reproductive effort of lower intensity. That concept has been formally quantified by Charnov and Krebs (1973).

Most osprey clutches contain 3 eggs (Bent 1937, p. 360). If

most osprey clutches contained 4 eggs, and if hatching and fledging success increased appropriately (as they apparently would; see the previous arguments concerning the ability of ospreys to incubate larger clutches, and the ability of larger broods of young to fledge successfully), individual ospreys would have a reproductive output that was substantially greater. For that greater annual reproductive effort to produce fewer young in the average lifetime of the adults, the increased clutch size would have to cause the average adult life-span to be shortened by more than 25%. That is, 3 years of producing 4 young per year produces as many young as 4 years of producing 3 young per year. There seems to be no evidence that any stress except heat stress incurred while hunting or flying in extremely hot weather could so drastically curtail an adult osprey's life expectancy. I have already rejected arguments that the male avoids hunting during substantial portions of the daylight hours to avoid heat stress or general fatigue. Consequently, I also reject the hypothesis that the current clutch-size of ospreys represents a long-term maximization of the number of young fledged due to trade-offs between clutch size and adult mortality.

The third hypothesis, that clutch-size is an attempt to minimize the probability of population extinction rather than an attempt to maximize individual reproductive output, has been argued most extensively by Mountford (1973). Mountford (1968) is also responsible for the fourth hypothesis, that there is an

interaction of a normal distribution of clutch sizes with a probability of recruitment that declines with increasing clutch size" (Stearns 1976, p. 17). While several of the assumptions and arguments made by Mountford (1968, 1973) in his 2 models could be cause for argument against his models, it is sufficient here to point out that both models require that evolution occur by group selection. Since it has been pointed out earlier that there are no known mechanisms by which group selection could affect the evolution of osprey reproductive effort, I reject both hypotheses.

The final hypothesis considered in this section is the model proposed by Gilbert and Butierrez (1973) to explain the life history of certain aphids. Stearns (1976, p. 16) points out that the "model works for an aphid population, where the members of groups are closely related, but for sexually outcrossing organisms the situation changes," and the model would not work. Since ospreys are sexually outcrossing organisms, I reject the hypothesis that the aphid life history model of Gilbert and Gutierrez (1973) could explain the evolution of the clutch size of the osprey.

The Significance of the Clutch Size of the Osprey

With various hypotheses about life history patterns, I have tried to explain the behavior of male ospreys which are responsible for feeding unfledged young. Every hypothesis about life history

patterns of which I am aware, is insufficient in some way or another to explain the observed time budget of the male osprey. In light of that, it seems appropriate to review the development of the current theories of life history patterns in an attempt to understand what modifications must be made if the theories are to be more generally useful.

Probably because birds are relatively easy animals to study, avian clutch size theory has played a major role in the development of animal population ecology. For the past 15 or more years, two viewpoints have dominated all discussion regarding the evolution of clutch sizes. Lack (1954, 1966, and elsewhere) has argued that evolution by means of individual selection has optimized the clutch size of all bird species. He argues that the clutch size corresponds to the maximum number of healthy young which the parents usually can rear; for birds with nidicolous young, that has been assumed to be the largest number of healthy young which can be fed adequately. More recent modifications of Lack's hypothesis have still incorporated his assumption that evolution by means of individual selection has optimized clutch size (e.g., Charnov and Krebs 1973). Wynne-Edwards (1962, 1964, and elsewhere) has argued instead that evolution by means of group selection has optimized the clutch size of some bird species. He argues that birds rear only the number of young needed to balance the population mortality, and not the maximum number of healthy young possible. More recent modifications of Wynne-Edwards' hypothesis have still

incorporated his assumption that evolution by means of group selection has optimized the clutch size (e.g., Mountford 1973). Nearly all discussion of clutch size theory has proceeded with the assumption that evolution (either by individual selection or by group selection) has optimized the clutch sizes of birds. Consequently, data which do not support optimizing individual selection have been declared, by default, to support optimizing group selection (e.g., Skutch 1976, Chapter 34).

However, there is a third hypothesis which has been virtually ignored in studies of avian reproductive ecology; that hypothesis is that evolution by means of individual selection has not optimized the clutch size of some birds, but merely has caused only operational clutch sizes of all birds to remain in existence. If no other individual is producing (on the average) more young, and if the individual in question is producing enough young to balance losses due to mortality, then natural selection will not select against that individual even if the maximum possible number of young are not being produced (as seems to be the case with ospreys).

Recent advances in other sectors of population biology are consistent with the idea that the hypotheses put forward by Lack and Wynne-Edwards are not the only viable hypotheses. Many studies with starch-gel electrophoresis have shown that most populations examined are not genetically homogeneous (e.g., Harris 1966, and

Lewontin and Hubby 1966; for a review, see Lewontin 1974). That result was not in accord with theoretical expectations which were also based on the assumption that only optimizing evolution was occuring.

The theoretical expectations were developed from the concept of genetic load. Genetic load is "the proportional amount by which the average fitness (or any other measurable trait) of a population is reduced relative to that of the optimal genotype" (Wallace 1975, p. 465). The concept was first introduced by Crow (1958), and since then has been followed to its logical conclusion, that populations of small or moderate size must be genetically homogeneous, by Kimura and Crow (1964). However, as mentioned above, most populations (regardless of size) are not genetically homogeneous. In resolving this apparent contradiction, Wallace (1968, 1975) has developed the concepts of "hard" and "soft" selection. Hard selection is natural selection which is acting independently of both the density and frequency of the genotypes in the population; non-optimal genotypes are always selected against, and only optimal genotypes are selected for. Lack, Wynne-Edwards, and most population ecologists have traditionally assumed that populations were experiencing essentially only hard selection. Soft selection, on the other hand, is natural selection which is acting relative to both the density and frequency of genotypes in the population; non-optimal genotypes are not selected

against if they are viable, and if optimal genotypes are absent from the population (or, in such low densities that the limiting resources which determine optimality are not yet limiting).

With respect to ospreys, brood size and fledging weights of osprey chicks are inversely correlated (Table XI). Underweight fledgling birds in general have a lesser chance of survival than do fledglings of normal weight (e.g., Lack 1966; Jarvis 1974). The male osprey with unfledged chicks hunts for only about one-third of the daylight hours, and apparently brings to the nest only enough food to feed 3, or occasionally 4, young adequately. Only 4 of the 7 young in the brood mentioned by Howe (1895) fledged. The female osprey seems to have adapted her clutch size to the male's behavior. Thus, a problem in osprey reproductive ecology is why the male hunts only for about one-third of the day. Since the rate at which the male brings fish to the nest does not vary with brood size or with the age of the unfledged chicks, it appears that male ospreys (at least in southeastern Virginia) have a behavioral tendency to hunt for only a fairly small, but constant, portion of each day.

Brown and Amadon's (1968, p. 199) statement that for ospreys with unfledged young "the average overall rate [at which fish are brought to the nest] is 3.8-4.6 fish per day, according to whether there are two or three young" is based entirely on Waterston's (1961) observations of only one nest for 2 successive years.

Their statement is contradicted not only by my observations, but also by Ueoka (1974) and MacCarter (1972) who also found that adults with small broods would bring as much food to the nest as would adults with large broods. That behavioral tendency seems neither maximal nor optimal.

The number of possible explanations of the history of such a tendency, and the number of possible answers to the question of why the male hunts only for about one-third of each day, are virtually unlimited. Elucidation of the cause(s) of the tendency is probably a moot point; the behavioral tendency exists, and its orgin is uncertain. However, attempts to explain the continued existence of such a non-optimal tendency apparently require that we incorporate the possibility of soft selection into our theories of life history patterns. Other life history phenomena, the continued existence of which seems to be explained only by recognizing the importance of evolution by means of soft selection, are the apparently sub-optimal clutch sizes reported for the North Atlantic gannet, Sula bassana, (Nelson 1964, 1966) and the glaucous-winged gull, Larus glaucescens (Vermeer 1963, cited by Lack 1966).

The possibility of non-optimal results from natural selection allows and requires re-interpretation and re-evaluation of many specific and general speculations in the literature. Hussell (1972, p. 361), in his thorough examination of Lack's hypothesis,

remarks that the "reduced success of experimentally enlarged broods does not [necessarily] support the idea that clutch size is limited by the environmental food supply because adaptive limitations of the birds' behavior or morphology could contribute to the same result." As has been argued in this thesis, the limitations of "the birds' behavior or morphology" do not necessarily have to be adaptive; analyses which have assumed the contrary possibly need to be re-interpreted.

Two general hypotheses which have been proposed about time-energy budgets are the principle of stringency (E.O. Wilson 1975) and the principle of allocation (Cody 1966; E.O. Wilson 1975). The principle of stringency is that "time-energy budgets evolve so as to fit the times of greatest stringency" (E.O. Wilson 1975, p. 142). The principle of allocation states that natural selection has acted "as that force which operates in the allocation of ... time or energy in a way which maximizes the contribution of a genotype to the following generations" (Cody 1966, p. 174). Since ospreys seem to be neither raising the maximum number of young possible nor experiencing any "stringent times", the universality of those 2 hypotheses appears to be invalidated. Broad generalizations based on these 2 time-energy budget hypotheses (e.g., E.O. Wilson 1975) are probably not as encompassing as might otherwise be hoped.

The assumption that evolution produces the optimal, essentially permeates the ecological literature (e.g., Slobodkin and Rapoport 1974; Smith and Fretwell 1974; Schaffer 1974; Brockelman 1975).

The significance of the clutch size of the osprey (at least in southeastern Virginia) is that it is apparently non-optimal. That is evidently due to the non-plastic and non-optimal behavior of the male osprey providing food for his unfledged young. Thus, the assumption of optimizing evolution in attempts to explain life history patterns does not always appear to be valid. One of the challanges now facing population biologists will be to determine the extent to which non-optimality pervades life history patterns of other organisms.

APPENDIX I

Description of Nest Sites

The osprey nests studied in this thesis were in Virginia in New Kent, York, and Mathews counties. The nest numbers correspond to the numbers assigned to the nests by Dr. Mitchell A. Byrd in his study of the Virginia osprey breeding population.

Nest 1 (New Kent county, West Point 7.5 minute Geological Survey quadrangle), on pilings in the York River near West Point, fledged 2 young in 1974; this nest was observed in 1974.

Nest 4 (York county, Poquoson West quadrangle), on a navigational aid in Wormley Creek, fledged 1 young in 1975; this nest was observed and visited to weigh the chick in 1975.

Nest 6 (York county, Claybank quadrangle), on stakes in the York River, fledged 1 (introduced) young in 1974 and no young in 1975; this nest was observed in 1974 and in early 1975.

Nest 7 (York county, Claybank quadrangle), on a navigational beacon in the York River, fledged 3 young in 1974; this nest was observed in 1974.

Nest 8 (York county, Claybank quadrangle), on a utility pole at the York River Naval Weapons Station, fledged at least 1 young in 1974; this nest was observed in 1974.

Nest 11 (Mathews county, New Point Comfort quadrangle), on a navigational beacon near Horn Harbor, fledged no young in 1974; this

nest was observed in 1974.

Nest 16 (Mathews county, New Point Comfort quadrangle), on a navigational beacon near Horn Harbor, fledged 3 young in 1974 and 2 young in 1975; this nest was observed in 1974 and 1975.

Nest 17 (Mathews county, New Point Comfort quadrangle), on a navigational beacon near Horn Harbor, fledged 2 young in 1974 and 3 young in 1975; this nest was observed in 1974 and 1975, and was visited to weigh the chicks in 1975.

Nest 20 (Mathews county, Mathews quadrangle), on an abandoned tarring platform beside Stokes Creek, fledged 1 young in 1975; this nest was visited to weigh the chick in 1975.

Nest 24 (Mathews county, Mathews quadrangle), on a navigational aid in Milford Haven, fledged 3 young in 1975; this nest was observed and visited to weigh the chicks in 1975.

Nest 25 (Mathews county, Mathews quadrangle), on a navigational beacon in the East River, fledged 5 young (1 introduced) in 1975; this nest was observed and visited to weigh the chicks in 1975.

Nest 35 (Mathews county, New Point Comfort quadrangle), on an old pier in Dyer Creek, fledged 3 young in 1975; this nest was observed and visited to weigh the chicks in 1975.

Nest 38 (Mathews county, Mathews quadrangle), on a duckblind in Milford Haven, fledged 4 chicks in 1975 (3 chicks were introduced from other nests, and 1 chick died prior to fledging); this nest was observed and visited to weigh the chicks in 1975.

Nest 43 (Mathews county, Mathews quadrangle), on a navigational aid in the East River, had 1 chick which died before it was 8 days old; this nest was observed briefly in 1975.

Nest 56 (Mathews county, New Point Comfort quadrangle), on a navigational beacon in the East River, fledged 2 chicks in 1975; this nest was observed and visited to weigh the chicks in 1975.

Nest 57 (Mathews county, New Point Comfort quadrangle), on a duckblind near Horn Harbor, fledged 1 chick in 1975 (1 other chick died before it was 8 days old); this nest was observed and visited to weigh the chicks in 1975.

Nest 62 (Mathews county, New Point Comfort quadrangle), on a navigational beacon in Davis Creek, fledged 1 chick in 1975; this nest was observed and visited to weigh the chick in 1975.

Nest 65 (Mathews county, New Point Comfort quadrangle), on a duckblind near Horn Harbor, fledged 1 (introduced) chick in 1975; this nest was observed and visited to weigh the chick in 1975.

Nest 66 (Mathews county, New Point Comfort quadrangle), on a duckblind in Harper's Creek, had 3 chicks which died when the nest was destroyed; this nest was observed and visited to weigh the chicks in 1975.

Nest 68 (Mathews county, New Point Comfort quadrangle), on a navigational beacon near Horn Harbor, fledged no chicks in 1974; this nest was observed in 1974.

APPENDIX II

Derivation of Equation for Calculating Relative Humidity

"Relative humidity is defined as the ratio of the partial pressure of the vapor in air to that of the saturated vapor at the same temperature" (Eskinazi 1975, p. 43). That is,

$$H_r = p_w/p_s, \tag{1}$$

where H_r is the relative humidity, p_w is the partial pressure of the water vapor in the air, and p_s is the pressure of saturated vapor in the air at the same temperature at which p_w is measured. The pressure of the saturated vapor can be calculated from

$$\ln p_s = 21.548 - (5388/T), \tag{2}$$

where T is air temperature in degrees Kelvin, and p_s is the pressure of saturated vapor in millibars of mercury (mb Hg) (Eskinazi 1975, p. 47). Equation (2) can be rewritten as

$$p_s = \text{antiln } [21.548 - (5388/T)], \tag{3}$$

where the units are the same as in equation (2). Equation (3) can be rewritten as

$$p_s = \{\text{antiln } [21.548 - (5388/t + 273)]\}/1.333224, \tag{4}$$

where t is dry-bulb temperature in degrees Centigrade, and p_s is now expressed in mm Hg (1 mm Hg = 1.333224 mb Hg).

The partial pressure of the vapor actually in the air can be calculated by

$$p_w = p'_s - [0.00066\ B\ (t - t')(1 + 0.00115t')], \tag{5}$$

where t' is wet-bulb temperature in degrees Centigrade, B is barometric pressure in mm Hg, and p'_s is the saturation pressure of water vapor at temperature t' (Humphreys 1920, p. 16). Since variation in B is relatively unimportant in determining p_w compared to variation in (t - t'), B is assumed to be 760 mm Hg (barometric pressure at 0 degrees Centigrade and standard gravity). By setting B = 760 mm Hg, equation (5) reduces to

$$p_w = p'_s - [(t - t')(0.5016 + 0.00057684t')]. \qquad (6)$$

In equation (6), p'_s is calculated from equation (4) at temperature t'. Relative humidity is then calculated by substituting equations (4) and (6) into equation (1) at temperature t. To calculate relative humidity, t and t' were measured at 15 minute intervals while observing the ospreys.

APPENDIX III

Weights and age at first weighing of young ospreys in 1975. (Before banding, individual identification was not possible, and consequently, weights are listed only in ascending order; after banding, individuals within a brood are identified by the last 2 digits of the individual's 8-digit band number.)

	Nest 4	Nest 20	Nest 24	Nest 25
Age at Initial Weighing	12 days	7 days	5, 7, and 9 days	7, 8, 14, 16, and 18 days
30 May	445 gm	330 gm	----	----
31 May	----	----	----	185, 260, 575, 675, and 720 gm
3 June	----	550 gm	180, 220, and 340 gm	----
8 June	----	950 gm	500, 570, and 670 gm	340, 540, 960, 1090, and 1270 gm
15 June	1420 gm	1290 gm	750, 930, and 980 gm	530, 930, 1255, 1275, and 1500 gm

	Nest 4 (continued)	Nest 20 (continued)	Nest 24 (continued)	Nest 25 (continued)
22 June	1590 gm	1380 gm	#31: 1070 gm	#34: 1490 gm
			#32: 1080 gm	#35: 1260 gm
			#33: 1300 gm	#36: 955 gm
				#37: 1210 gm
				#38: 1650 gm
29 June	1560 gm	1710 gm	#31: 1340 gm	#34: 1220 gm
			#32: 1650 gm	#35: 1260 gm
			#33: 1490 gm	#36: 1170 gm
				#37: 1290 gm
				#38: 1370 gm
7 July	1635 gm	1715 gm	#31: 1565 gm	#34: fledged
			#32: 1520 gm	#35: 1330 gm
			#33: 1455 gm	#36: 1425 gm
				#37: fledged
				#38: fledged
11 July	fledged	1715 gm	#31: 1570 gm	#34: fledged
			#32: 1405 gm	#35: 1345 gm
			#33: 1385 gm	#36: 1450 gm
				#37: fledged
				#38: fledged

	Nest 4	Nest 20	Nest 24	Nest 25
	(continued)	(continued)	(continued)	(continued)
16 July	fledged	fledged	all fledged	#34: fledged
				#35: fledged
				#36: 1375 gm
				#37: fledged
				#38: fledged
20 July	fledged	fledged	all fledged	all fledged

	Nest 35	Nest 38*	Nest 66
Age at Initial Weighing	18, 20, and 22 days	4, 5, 7, 7, and 8 days	6, 7, and 9 days
31 May	----	----	145, 235, and 275 gm
3 June	----	40, 75, 250, 290, and 370 gm	----
8 June	490, 790, and 950 gm	90, 180, 590, 600, and 700 gm	485, 635, and 835 gm
15 June	1010, 1250, and 1355 gm	425, 940, 950, and 1060 gm	965, 1030, and 1360 gm
22 June	#41: 1380 gm #42: 1570 gm #43: 1650 gm	850, 1200, 1290, and 1320 gm	nest destroyed and chicks missing

* 1 chick died between 8 and 15 June 1975.

	Nest 35 (continued)	Nest 38 (continued)	Nest 66 (continued)
29 June	----	#29: 1430 gm	----
		#30: 1070 gm	
		#31: 1300 gm	
		#32: 1350 gm	
7 July	#41: 1510 gm	#29: 1465 gm	----
	#42: 1565 gm	#30: 1325 gm	
	#43: 1625 gm	#31: 1375 gm	
		#32: 1260 gm	
11 July	#41: 1435 gm	#29: 1505 gm	----
	#42: 1525 gm	#30: 1175 gm	
	#43: fledged	#31: 1295 gm	
		#32: 1245 gm	
16 July	all fledged	#29: fledged	----
		#30: 1245 gm	
		#31: fledged	
		#32: fledged	
20 July	all fledged	#29: fledged	----
		#30: 1195 gm	
		#31: fledged	
		#32: fledged	
27 July	----	all fledged	----

	Nest 17	Nest 62
Age at Initial Weighing	34, 36, and 38 days	23 days
16 July	#58: 1495 gm #59: 1675 gm #60: 1595 gm	905 gm
20 July	#58: 1605 gm #59: 1645 gm #60: 1575 gm	1205 gm
28 July	all fledged	1245 gm
4 August	----	1275 gm
14 August	----	fledged

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